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A Tropical Caterpillar that Mimics Faeces, Leaves and a Snake (Lepidoptera: Oxytenidae: *Oxytenis naemia*)

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Abstract. The tropical moth *Oxytenis naemia* shows four different mimicry strategies during its life, including characteristics such as false eyes and snake-like display. The uniqueness of the combination of these mimetic strategies reflects a high selection pressure, which appears to be typical for tropical ecosystems.

Introduction

It is a widespread phenomenon that some animals are inconspicuous because they resemble naturally occurring objects like bark, a leaf, a twig, or inedible objects. This phenomenon is termed mimicry (Edmunds, 1981) and serves to help the animal escape detection by predators or prey. When insects at first resemble objects of a limited size (e.g. ants) subsequent instars of the species must mimic different objects. Many praying mantids have first instars which resemble ants, whereas later instars and the adults mimic leaves, grass blades or bark (Edmunds, 1976). In holometabolous insects, which pass through morphologically different life stages, each stage can mimic a different model. Caterpillars and sphingid, geometrid and bombycid moths are especially well known for changing their mimicry strategy during their lives (Cott, 1940). The present case deals with *Oxytenis naemia* Druce, 1906, (Oxytenidae), a moth of tropical Panama.

Materials and Methods

The moth *Oxytenis naemia* is a representative of the strictly neotropical family Oxytenidae (superfamily Bombycoidea) which contains some 36 species. *Oxytenis* moths are mainly brown and yellow (Watson and Whalley, 1975) and most of them resemble dry leaves when resting. *Oxytenis naemia* is known from tropical Costa Rica and Panama to Peru and Paraguay. It is a medium-sized moth which lays its eggs exclusively on the leaves of a few species of Rubiaceae shrubs, mainly *Isertia haenkeana*.

The study was carried out in the vicinity of Gamboa, Panama, in a tropical lowland forest. Approximately 50 oxytenid larvae were collected

from several locations near Gamboa between August and October 1983 and were individually raised on leaves of *Insertia haenkeana* (Rubiaceae) in the laboratory (25-32°C, 75% r.h., LD 12:12; = standard Gamboa conditions, Nentwig, 1985).

Results

Oxytenis larvae of instars one-three are black and have many small spines and a short, forked tail. Their resting position is in the form of a "J", the anterior part of the body being bent towards the first abdominal segments and touching them. In this position the head is concealed and the whole animal resembles bird dung. In all instars of *O. naemia* the third thoracic segment is enlarged and forms small wing-like structures. These structures camouflage the overall shape of the caterpillar and emphasize the general impression of a bird's dropping (Fig. 1a). The fourth instar differs in colour from the foregoing stages. The larvae are rather brown, often quite light, sometimes yellowish, and appear somewhat oily, so resembling the faeces of some other animal, probably a large bird. These faeces-like instars last altogether approx. 10-14 days.

In the fifth and final instar (duration 4-9 days) the caterpillar changes its mimicry strategy again and resembles a fallen, rolled-up leaf. This effect is produced by a triangular pattern on the front part of the body which gives the impression of the open end of a rolled leaf. The main colour is now a velvet brown; some parts of the caterpillar are light to dark brown, but the whole animal may instead be velvet green, red-brown or pink (Fig. 1b). Thus some of the fifth instar caterpillar population mimic freshly fallen green leaves and others resemble dried or drying leaves. There are additionally triangular patterns on the sides of the abdomen. In most individuals they are divided into single spots or else they are completely lacking (Fig. 2). These spots are sometimes darker than the caterpillar thus resembling holes in the leaf. In other larvae they are silver-white (especially if the larva is green) and may resemble a fungus infection, or small faeces dots.

When these leaf-mimicking caterpillars are disturbed most do not form a "J" (which would not suit the strategy of mimicking a rolled-up leaf), but instead show a curious display which has been described independently by several observers as "snake-like". Two spots located dorsally on the enlarged thoracic section resemble a pair of half-closed eyes. By pumping haemolymph into the thorax, a fold of the thoracic skin is expanded and the eye spots enlarge. These large false eyes now consist of a black pupil with a yellow iris and even show a touch of white in the upper corner. This gives the impression of light reflections as in a real vertebrate eye (Fig. 1c). Sometimes the caterpillar rears up and waves the anterior third of the body. In this posture a pair of bright yellow spots on the underside of the enlarged thoracic part becomes exposed. These are

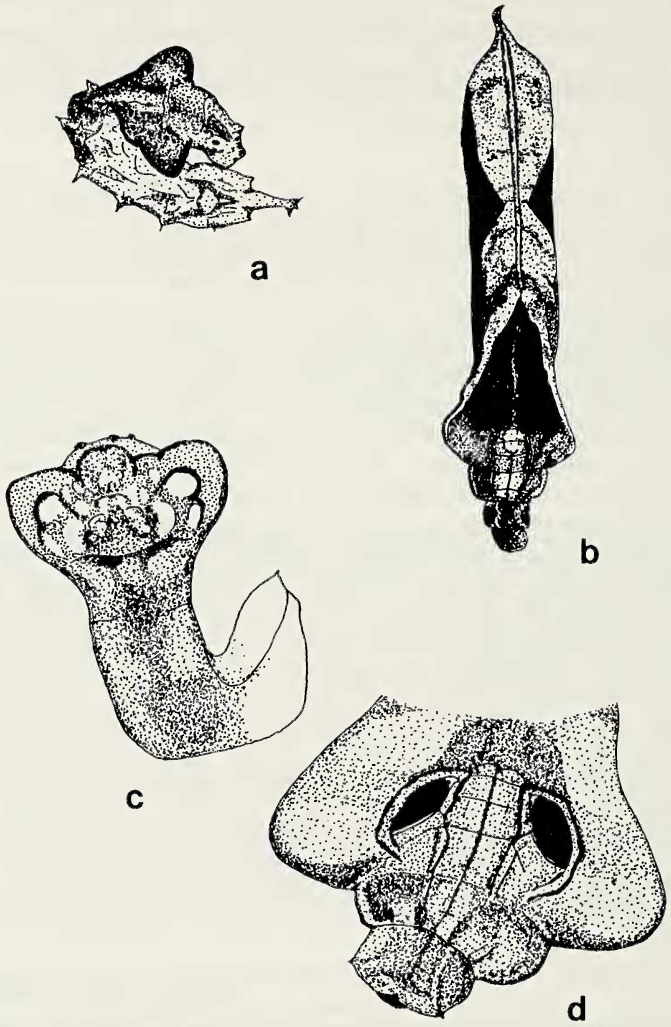

Fig. 1. The mimicry strategy of *Oxytenis naemia* caterpillars: (redrawn schematically from slides).

a. The third larval instar mimics dark faeces (dorsal view).
b. The third larval instar mimics a rolled-up leaf (dorsal view).
c. When the caterpillar is disturbed, large false eyes appear on the thorax (fifth instar, anterior view).
d. When more disturbed, the caterpillar rears up, waves the anterior third of the body, and shows additional false eyes on the underside (fifth instar, dorsal view).

Caterpillar length ca. 20 mm (a) and 40-50 mm (b-d).

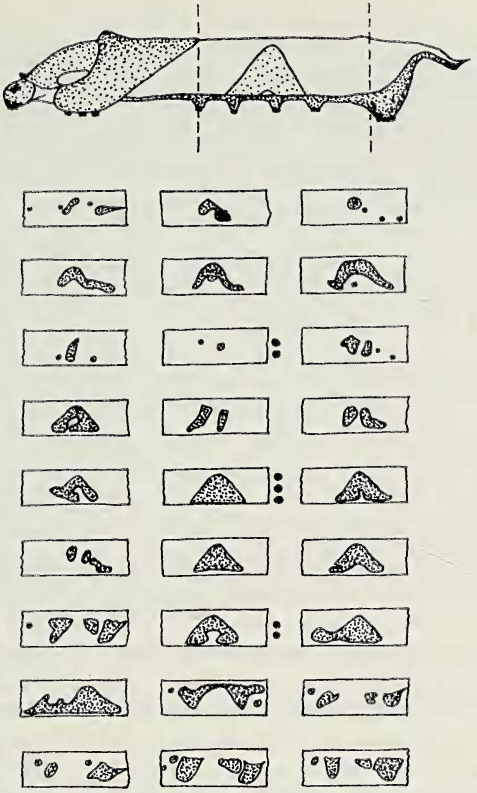

Fig. 2. Fifth instar of *O. naemia* (lateral view, schematically), showing the high variation of the lateral patterns (area between the dotted lines). Dots mark patterns which occurred twice or three times; three larvae had no patterns.

certainly imitations of eyes as well (Fig. 1d). The opening of the false eyes and the turning behaviour is so impressive that Hingston (1932) who saw it in the Guiana forest described it as a cobra display.

Finally, after the prepupal stage (one day) and pupal stage (9-14 days) the moth ecloses. In colour pattern and posture of the wings the resting moth resembles a dry, fallen leaf. This mimicry includes the normal movement of a falling leaf. When disturbed, only a small number of *O. naemia* specimens move their wings like a normal moth or butterfly. Most fall to the ground, holding their wings in the resting position (Aiello, pers. comm.), and 'disappear' in the litter layer like a real dead leaf, completely escaping one's view.

Discussion

Oxytenis naemia possesses four different mimicry strategies. First they resemble 1) small, dark faeces; next 2) large, lighter faeces; then 3) rolled leaf and flat leaf. In addition, 4) morphological and behavioural adaptations enable the animal to show false eyes and a snake-like appearance. The adults resemble dead leaves and appear to fall to the ground when disturbed. All these capabilities are known from other caterpillar species, but it is unique to find them all realized in one species. Curio (1965) reports snake-mimicry in the neotropical sphingid *Pholus labruscae*. Moss (1920) studied the Brazilian sphingid *Leucorampha ornatus*, which in addition to a snake-like display enlarges the thorax and shows its underside, where two dark, symmetrical eye-spots appear. Such behaviour and mimicry is usually explained as a response to strong predator pressure. The same is indicated by the irregular distribution of the caterpillars over their one food plant. Over large areas *O. naemia* larvae are absent, then they occur on one shrub in a relatively high density (three to five larvae). The larvae in these groups are of the same age, which reflects the special oviposition behaviour of the female moth. The changes in shape, colour and general appearance of the larvae may make it difficult for a predator to obtain a search image for larvae of this species. Moreover, this is accentuated by a variable behaviour: some larvae form a "J", some do not, and some show snake display. The colour pattern is highly variable in the last instar, as well as in the adult moths. In the genus revision, Jordan (1924) has noted that the typical three black dots on the male forewing are sometimes absent but he was not aware of the full range of variation in colouring. In males, wings vary from a bright brown to the common dark, greyish brown. Females also vary from a dark, male-like colour to a more typical light brown.

The population losses due to parasites were high among the sample larvae (these had been collected in the field and raised in the laboratory). An unidentified microorganism (possibly a virus) was present in 21% of the individuals and had the effect of changing the internal consistency of the pupae to a muddy liquid within a few days. Another further 21% of the original larval population (= 33% of the surviving pupae) were parasitized by a tachinid fly (1-10 flies per pupae, average = 4.0). On one occasion these flies were observed attacking a leaf-mimicking instar of *O. naemia* in the field. The caterpillar defended itself successfully by the snake-like display indicating that the interpretation of this behaviour exclusively as a cobra display (Hingston, 1932) is perhaps too restrictive. It is difficult to imagine that a 50-mm-caterpillar mimics a snake, especially a cobra on a leaf, as defence against a parasitic fly. The main parasitism by the tachinids occurs in the early faeces-mimicking instars which do not show the snake-like behaviour. This leads to the conclusion that the latter display is not directed against parasites, but probably

towards potential vertebrate predators. Arboreal venomous vine snakes occurred frequently in the study area, some of which are small—at least when young. Curio (pers. comm.) points out that the head of some poisonous snakes are very small, and, in many cases, the full body length of the snake cannot be seen. Thus, the 50-mm-caterpillar would represent only the visible part of a much longer snake. Generalized eye-spot markings as a defence mechanism are wide-spread in the animal kingdom (Wickler, 1968) and their anti-predator effect has been demonstrated (Blest, 1957). Consequently, it may be difficult to discriminate between a specialised snake display and a more generalized anti-predator behaviour, where snake-like movements are only one feature among other frightening characteristics.

The multiple mimicry strategy of *O. naemia* supports earlier assumptions (e.g., Dobzhansky, 1950; Robinson, 1978) that in tropical ecosystems predator pressure, parasitism, and other interspecific actions are the main cause of mortality. Here they are held to be the major selective force, whereas temperate zones climatic conditions are thought to be more important. In the tropics mimicry phenomena are extremely common, and interactions between species can be very complex. Further research will certainly reveal additional equally bizarre examples of protective colouration and behaviour.

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